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Macroderma gigas.

By Wendy Starr Hudson and Don E. Wilson

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Macroderma Miller, 1906

Macroderma Miller, 1906:84. Type species *Megaderma gigas* by original designation.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Megadermatidae. The genus *Macroderma* contains only one Recent species, *M. gigas*, and a fossil form, *M. godthelpi* Hand (1985).

Macroderma gigas (Dobson, 1880)

Ghost Bat

Megaderma gigas Dobson, 1880:461. Type locality Mount Margaret, Wilson's River, central Queensland, Australia.

CONTEXT AND CONTENT. Context same as for genus. Douglas (1962) named *M. g. saturata* on the basis of specimens from Kalumburu in northern Western Australia, but Koopman (1984*a*) synonymized it with the nominate form.

DIAGNOSIS. The upper incisors are absent as in all megadermatids, but the rudimentary premaxillae are more highly developed in *Macroderma* than in *Megaderma*. *M. gigas* lacks P2, in contrast to species of *Megaderma* (Miller, 1906). As in other members of the family, the mesostyles of M1 and M2 are displaced lingually, more so in *Macroderma* than in *Lavia* or *Cardioderma*. Reduction or loss of the hypoconulid of m3 characterizes the family, but *Macroderma* has a better developed m3 hypoconulid than other genera in the family (Hand, 1985). The shield-like interorbital expansion (Fig. 1) is intermediate in size between that of the Asian and African megadermatids. The postorbital and antorbital processes are more prominent than in *Megaderma*, but less so than in *Cardioderma* and *Lavia* (Miller, 1907). The interpterygoid space extends to the level of the posterior border of M2. The posterior lobe of the tragus is proportionally shorter than that of *Megaderma* and the anterior lobe is much broader at the base, more convex anteriorly, and obtuse at the tip (Dobson, 1880). The second finger extends beyond the middle of the first phalanx of the third finger, in contrast to the shorter second finger of *Megaderma spasma*. The tail consists of only two vertebrae hidden between the two integumentary layers of the large interfemoral membrane. Short hairs cover the extremity of the carpus, thumb, and propatagium.

GENERAL CHARACTERS. The Australian ghost bat, *M. gigas*, with a body mass from 130 to 170 g (Kulzer et al., 1984; Pirlot and Nelson, 1980; Taylor, 1984), is one of the largest of the microchiropterans. Head and body length ranges from 100 to 140 mm and forearm length from 105 to 115 mm (Nowak and Paradiso, 1983). The long ears join along the midline for half the length of their inner margin (Fig. 2). The noseleaf is long and has convex sides and its anterior concave disk is large with a vertical process above (Troughton, 1926). The eyes are relatively large for microchiropterans and the claws are strong and curved (Taylor, 1984). The lower lip projects farther than the upper and the nostrils are depressed within an area of naked skin. In most populations, the terminal third of the dorsal hairs is pale grayish brown, and the pale white of the ventral pelage matches the ears, noseleaf, and membranes (Troughton, 1926). The species also encompasses individuals with darker fur and membranes (Koopman, 1984*a*). The wing span of *M. gigas* is approximately 0.6 m (Breeden and Breeden, 1967). The female is smaller than the male, although the measurements of the tibia and first phalanx of the fifth finger are greater in the female (Waite, 1900).

External measurements (in mm) of the male holotype and of a female from the Australian Museum (Waite, 1900) are: head and body length, 135, 110; head length, 48.5, 41.0 (broken); ear length, 56, 47; length of anterior lobe of tragus, 12, 10; length of posterior lobe of tragus, 25.5, 22.0; length of noseleaf, 16, 15; length of forearm, 117.0, 103.5; length of thumb, 21.0, 19.5; length of metacarpal II, 84.5, 80.5; length of phalanx II, 16, 17; length of metacarpal III, 69, 68; digit III, length of phalanx I, 47, 44; digit III, length of phalanx II, 92, 80; length of metacarpal IV, 79, 78; digit IV, length of phalanx I, 25.5, 24.5; digit IV, length of phalanx II, 38.5, 33.0; length of metacarpal V, 84.5, 82.0; digit V, length of phalanx I, 32, 33; digit V, length of phalanx II, 28.5, 23.5;

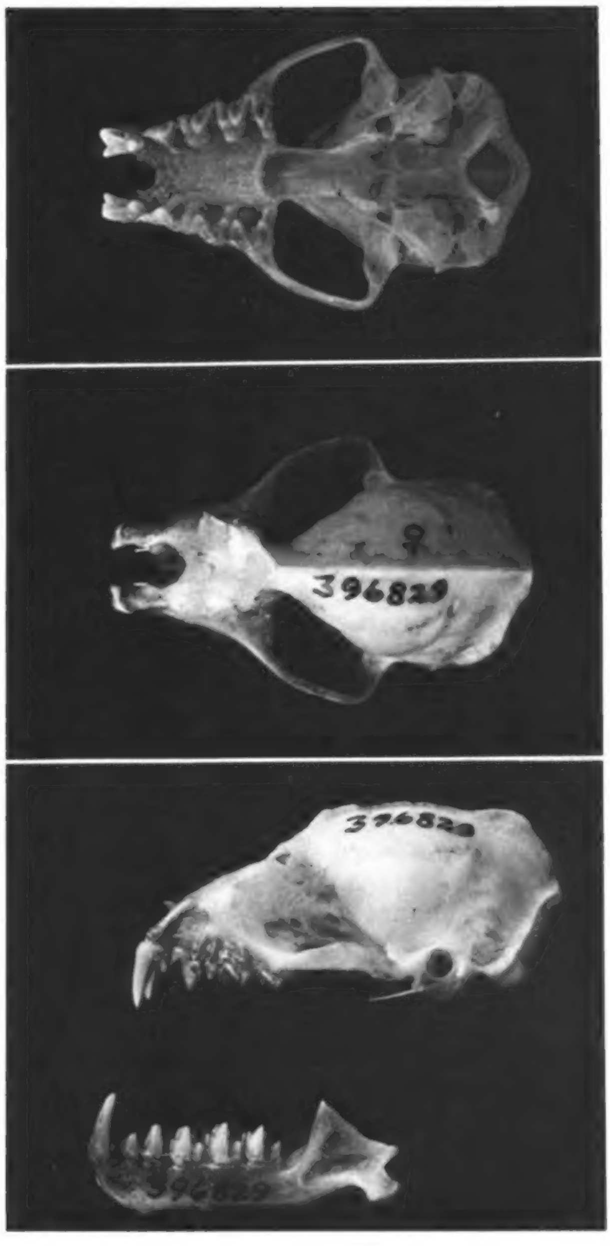

FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of female *Macroderma gigas*, USNM 396829. Greatest length of skull is 38.7 mm.

FIG. 2. *Macroderma gigas* photographed in Australia by Frank Greenwell in 1973.

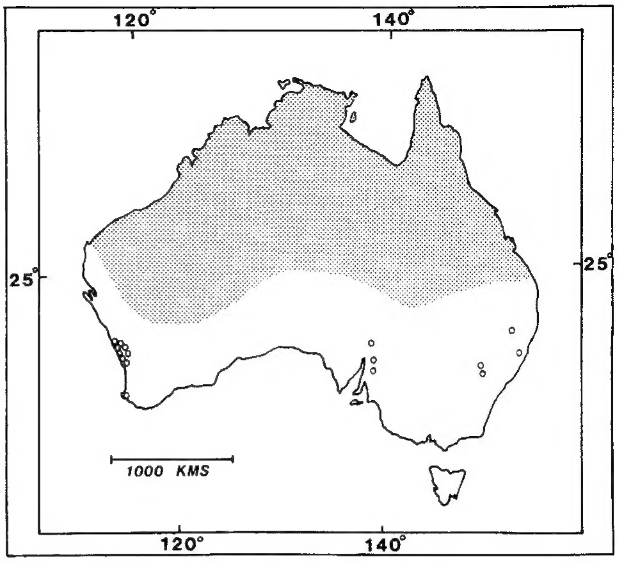

FIG. 3. Distribution of *Macroderma gigas* (shaded area). Open circles denote extralimital localities from which Holocene fossils are known.

tibia length, 44, 45; calcaneum length 28.5, 28.0; and length of hindfoot, 28.5, 23.5.

Douglas (1962) listed the following skull measurements (in mm) for a specimen from Western Australia: length, 38.5; breadth, 24.3; interorbital constriction, 4; and palate, 13. Molnar et al. (1984) described several fossil specimens referable to the Recent species, and listed the following measurements (in mm) for a Recent specimen from the Queensland Museum; length of mandibular ramus, 29.2; length and width of p4, 3.2, 1.9; length and width of ml, 3.5, 2.6; length and width of m2, 3.7, 2.6; length and width of m3, 3.6, 2.4.

DISTRIBUTION. *Macroderma* presently occurs throughout the northern two-thirds of Australia south to 28°S in Western Australia and 27°S in western Queensland (Fig. 3). It is found both in dry country and in humid rainforests (Molnar et al., 1984). A sighting on Mt. Kenneth, Western Australia, in 1854 is the southernmost record; however, most records at the southern limits consist of isolated individuals rather than permanent populations. Records of large, permanent populations at the southern border of its range extend from the Pilbara district in Western Australia to Mt. Etna in Queensland (Molnar et al., 1984). Pleistocene localities coincide with the present distribution only in northeastern Queensland. *Macroderma* occurred much farther south in the Pleistocene than it does today (Cook, 1960). Finlayson (1961) considered the species to be relictual in central Australia and suggested that its range is receding from the south. Baynes et al. (1976) suggested that the absence of dry, smooth-walled caves in southern Australia limits its range. The genus may occur in suitable habitat in New Guinea (Filewood, 1983), although no specimens have been taken there.

FOSSIL RECORD. The most southerly fossil occurrence is approximately 600 km SSW of Mt. Kenneth, Western Australia, the southernmost record of living ghost bats. The Wanneroo-Yanchep region has yielded occasional skeletal material and may represent only a recent southward expansion of the range of the species (Bridge, 1975). Large guano piles and skeletal material were found at the Ledge Point-Dongara and Coorow-Watheroo areas. Bridge (1975) suggested that the distribution and abundance of the guano piles and skeletal material represent expansions and contractions of the range during the Holocene.

In Drover's Cave, Lundelius (1960) discovered *M. gigas* remains at all depths up to 1.5 m in association with rodent and marsupial material. Subfossils have been collected from limestone caves in Western Australia and the Flinders Ranges of South Australia (Hamilton-Smith, 1974).

All fossil specimens found to date seem to differ only in minor ways from modern representatives of the species (Molnar et al., 1984). Analyses of current and past distribution patterns suggest the possibility of successive waves of expansion and contraction of range, perhaps related to changing climatic conditions (Bridge, 1975; Molnar et al., 1984).

FORM. Although the predominant pelage color is pale gray or whitish, the relatively long and lax hair ranges in color from almost white through shades of gray to almost brown (Douglas, 1962).

Although most species of bats have only a single pair of pectoral mammae, *Macroderma* has a pair of inguinal "false mammae" which serve as holdfasts for the young, in addition to the normally functioning pectoral pair.

The skeletal arrangement in the thoracic region is somewhat unusual in megadermatids. The anteriorly widened presternum is fused to the first pair of ribs, the first thoracic vertebra, and the seventh cervical vertebra to form a solid ring of bone (Miller, 1907). The pelvic girdle is more like that of other microchiropterans, with the ischia free posteriorly. The thread-like fibula is only half as long as the tibia (Koopman, 1984*b*).

A distinct sagittal crest frequently develops on the large, robust skull of older individuals. The pentagonal frontal shield is flat and its angles are defined distinctly.

The dental formula is i 0/2, c 1/1, p 1/2, m 3/3, total 26. The teeth are large, robust, and highly cuspidate. The metastyle of M1 has shifted posteriorly, and the mesostyle, almost obliterated, has shifted lingually between the parastyle and the metacone. The anterolingual cingular cusp of C1 is greatly developed (Andersen and Wroughton, 1907).

Volumes of 11 brain structures indicate that *M. gigas* is intermediate between insectivorous microchiropterans and the carnivorous species from South America (Pirlot and Nelson, 1980). *M. gigas* is the least encephalized member of its family with an encephalization index of approximately 142 (Stephan et al. 1981). Stephan and Nelson (1981) described *Macroderma* as having a clear midbrain exposure, a large hemispherical part of the paraflocculus, and a relatively small lobulus petrosus. Compared to other species of bats, higher development of the brain was indicated by the partial cover of the midbrain, traces of a dorsal sulcus, and a well-developed cerebellum (Stephan and Nelson, 1981).

FUNCTION. Body temperature is maintained between 35 and 39°C at ambient temperatures of 0 to 35°C. Oxygen consumption increases above and below the thermal neutral zone, 30 to 35°C. As ambient temperatures decrease to 25°C, sufficient oxygen is obtained through an increased depth of breathing. Below 25°C, the breathing rate is directly proportional to oxygen consumption. At 20°C, elevated oxygen requirements of the tissues are met by increased stroke volume, the arteriovenous difference in the blood, and shivering. Within the thermal neutral zone, heart rate remains

minimal and increases with oxygen consumption. The species does not hibernate or undergo daily torpor (Leitner and Nelson, 1967).

When a *Macroderma* is moving towards detected prey, it emits echolocation pulses that are shorter in duration and average 0.8 ms (n = 11); duration increases to a mean of 1.7 ms (n = 13) during landing (Kulzer et al., 1984).

Macroderma has unusually good vision for a microchiropteran, with a spatial resolution approaching two cycles/degree based on retinal morphology (Guppy and Coles, 1983). It may well use vision extensively to locate or discriminate prey.

Mastication is thorough and passage through the digestive system is slow compared to fruit-eating bats (Douglas, 1967). *M. gigas* also may be able to balance their water budget without recourse to free drinking water (Kulzer et al., 1984).

Douglas (1967) described a musty odor from *Macroderma* that he could distinguish readily from that of other species.

ONTOGENY AND REPRODUCTION. Females congregate in maternity colonies during the breeding season and each gives birth to a single young at the end of the breeding season (Thornback and Jenkins, 1982). The breeding season is late October to early November in the south and somewhat earlier in the far north (Thornback and Jenkins, 1982). In the Pilbara District, Douglas (1967) found a female with an embryo 10 mm in crown-rump length in August, and three others with embryos of 52, 65, and 70 mm in October. In November, he found neonates ranging from 60 to 80 mm in length. In the Northern Territory, he found a 45-mm embryo in June, and a hairless neonate of 96 mm in September. The flaccid pectoral and inguinal mammae of nulliparous *Macroderma* become turgid after pregnancy. The mammae and clitoris are more easily detected in parous than in nulliparous females (Douglas, 1967).

ECOLOGY. Although buildings may be used as feeding stations, *Macroderma* roosts only in caves, rock crevices, and mines (Douglas, 1967). Colonies of up to several hundred individuals may form, but small groups or individuals are more common (Taylor, 1984).

Macroderma gigas feeds on mice, small bats, small birds, legless lizards (Pygopodidae), geckos (Gekkonidae), small snakes, and insects. *Mus musculus* remains were found most commonly in discarded food material in caves of the Pilbara District. Twenty species of birds also were identified in the material (Douglas, 1967). Wilson (1973) classified *Macroderma* as primarily a specialized carnivore and as a foliage gleaner secondarily. The occasional finding of large quantities of insect chitin in the stomachs of *M. gigas* suggests that the bat is an opportunistic feeder (Kulzer et al., 1984). Vestjens and Hall (1977) reported termites in the stomach of one individual. Live prey is eaten more frequently and normally is eaten near the point of capture (Douglas, 1967).

The ghost bat has few natural predators, Medium-sized owls (Strigidae) compete for insects and small mammals, but no correlation exists between presence of these owls and *Macroderma*. Local movements of colonies and individuals most likely result from fluctuations in prey availability (Molnar et al., 1984).

Although the range seemingly has contracted during the Holocene Period, probably several thousand *Macroderma* remain alive. Some areas of southern Australia underwent a transition from open savanna to dense woodland during the Pleistocene and Recent. These changes may have led to the contraction of the range of the species in Australia (Thornback and Jenkins, 1982). The species is threatened by vandalism (McKean and Price, 1967), mining of limestone caves, and quarrying (Hamilton-Smith, 1980). There are few national parks or reserves to provide refugia (Hamilton-Smith, 1980). *M. gigas* is classified as a vulnerable species by the International Union for the Conservation of Nature and Natural Resources (Thornback and Jenkins, 1982).

A species of tick, *Argas (C.) macrodermae*, was described in 1977 from specimens of the ghost bat (Hoogstraal et al., 1977). Douglas (1967) suggested that *Macroderma* is conspicuously free of ectoparasites in comparison with other microchiropterans. The only reported endoparasite is a filarial nematode, *Josefilaria mackerrasae* (Moorhouse et al., 1979).

BEHAVIOR. *Macroderma* is inactive during daylight hours and leaves the roost from one to several hours after sunset. Some individuals may remain in the roost all night. They leave singly, in pairs, or in small groups. During flight, they hold the head high and appear to scan the countryside (Douglas, 1967). Hunting behavior began 3 to 5 h after dark in a captive colony (Kulzer et al., 1984). The bats use a sit-and-wait hunting strategy. From roosts, the bats look in the direction of noises from prey and direct their pinnae to detect movement. Hearing is used initially to detect prey, and perch position is altered occasionally to "listen" to prey from a different angle. Echolocation emissions reach a peak frequency before the bat flies and hovers over prey. The precise location of the prey is attained through a pulse series emitted during a variable number of reconnoitering flights over potential prey. When located, the victim is seized quickly from above, pressed to the ground, and held by the thumb claws for the killing bite into the neck or head delivered by the canine teeth. Small mammals are manipulated by the thumb claws and eaten from head to tail (Guppy and Coles, 1983).

Captive *M. gigas* can capture prey up to 80% of their body mass. When able to catch large prey, *Macroderma* may not hunt daily (Kulzer et al., 1984).

When food is scarce under captive conditions, two or more individuals may fight to obtain the same prey item. While fighting, they emit high-pitched squeals (Douglas, 1967). They often produce a cricket-like chirp when hungry and the young continuously chirp when separated from the mother. Usually, the bats make no noise at all (Douglas, 1967).

Human intruders to a cave colony may cause the group to become nervous and leave inconspicuously (Douglas, 1967).

The extent of daily and seasonal movements is unknown, but Douglas (1967) suggested that there were differences in night roosting behavior during wet and dry seasons. During the wet season, bats at Kulumburu frequented buildings as feeding roosts, but were not known to do so during the dry season.

GENETICS. Nothing is known about the genetics of this species.

REMARKS. The name *Macroderma* is from the Greek roots *makros*, meaning large, and *derma*, meaning skin. The specific epithet *gigas* is Greek, meaning giant, and refers to the fact that this is the largest species in the family.

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Editors of this account were B. J. VERTS and SYDNEY ANDERSON. Managing Editor was TIMOTHY E. LAWLOR.

W. S. HUDSON AND D. E. WILSON, WELLS COLLEGE, AURORA, NEW YORK 13026 AND U. S. FISH AND WILDLIFE SERVICE, NATIONAL MUSEUM OF NATURAL HISTORY, WASHINGTON, D.C. 20560.